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CROP RESPONSES TO CARBON DIOXIDE DOUBLING: A LITERATURE SURVEY*

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ABSTRACT

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Atmospheric carbon dioxide (CO_2) concentration will probably double by the middle of the next century. Since this is widely expected to increase crop yields, the Department of Energy has established a research program to gather data on the effects of CO_2 on plants and to develop models that can be used to predict how plants will behave in a future high-CO_2 world.

This paper identifies strengths and weaknesses in the knowledge base for modelling plant responses to CO_2. It is based on an extensive tabulation of published information on responses of ten leading crop species to elevated CO_2. The response variables selected for examination were: (a) net carbon exchange rate, (b) net assimilation rate, (c) biomass accumulation, (d) root:shoot ratio, (e) harvest index, (f) conductance, (g) transpiration rate and (h) yield. The results were expressed as a predicted percentage change of the variable in response to a doubled CO_2 concentration. In most instances, a linear model was used to fit the response data.

Overall, the net CO_2 exchange rate of crops increased 52% on first exposure to a doubled CO_2 concentration, but was only 29% higher after the plants had acclimatized to the new concentration. For net assimilation rate, the increases were smaller, but fell with time in a similar way. The C_4 crops responded very much less than C_3 crops. The responses of biomass accumulation and yield were similar to that for carbon fixation rate. Yield increased on average 41% for a doubling of CO_2 concentration. The variation in harvest index was small and erratic except for soybean, where it decreased with a doubling of CO_2 concentration. Conductance and transpiration were both inversely related to CO_2 concentration. Transpiration decreased 23% on average for a doubling of CO_2.

Crop responses to CO_2 during water stress were variable probably because high CO_2 both increased leaf area (which increases water use) and reduced stomatal conductance (which decreases water use). However, low nutrient concentrations limited the responses of most crops to CO_2. The absolute increase in photosynthetic rate in response to high CO_2 concentration was always greater in high light than in low light, but this was not necessarily true of the relative increase. In all except one study, responses to CO_2 were larger at high temperature than at low. Most of these studies were done in high light intensity. In low light intensity, the effect of temperature on the CO_2 response was smaller.

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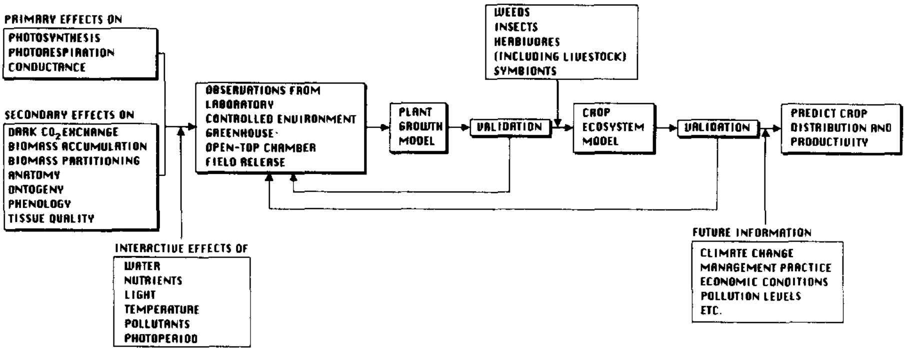

Fig. 1. Logic diagram for data acquisition, model development and eventual prediction of future effects of elevated CO_2 on agriculture.

These tables highlight the paucity and variability of data on interactions between CO_2 and other environmental variables. Given that C_4 plants already possess a CO_2-concentrating mechanism, they have a surprisingly large response to CO_2. Apart from the obvious difference between C_3 and C_4 plants, it was not possible to further subdivide plants into groups based on their responses to CO_2.

INTRODUCTION

Atmospheric carbon dioxide (CO_2) concentration is increasing (Keeling, 1983) and is expected to double from the current mean value of 340 parts per million by volume (p.p.m.) to 680 p.p.m. before the end of the next century (U.S. National Research Council, 1983). The United States government has been sponsoring research on the potential impact of this change for many years and in 1978 it passed the National Climate Program Act which named the Department of Energy (DOE) as the lead agency to coordinate this research. The DOE has established research programs covering: (1) the carbon cycle, (2) climate effects, (3) vegetation response and (4) indirect effects.

The purpose of the DOE's Vegetation Response Research Program is to develop the ability to predict the responses of crops and ecosystems to elevated CO_2 concentrations (Dahlman et al., 1985). The approach is, first, to acquire laboratory and field data on the effect of CO_2 on plant growth and pathogens are theoretically controllable, there are a multiplicity of plants, agricultural ecosystems and unmanaged ecosystems to CO_2 and other environmental variables which themselves may change as CO_2 concentration increases.

Elevated CO_2 concentrations are widely expected to increase crop photosynthesis and yield. The possibility of significantly increased crop yield is of distinct economic and social interest and this has sparked a wave of interest in the agricultural research community. The purpose of this paper is to help identify the strengths and weaknesses in the knowledge base for processes that are important for modelling and predicting crop growth in a future high-CO_2 world.

Figure 1 represents the logic of the DOE Vegetation Response Program for data acquisition, model development and eventual prediction of CO_2 effects on agriculture. Even for a crop monoculture, in which insects, weeds and pathogens are theoretically controllable, there are a multiplicity of factors and interactions which require understanding before accurate predictions can be made about the possible effects of increased CO_2.

This paper is based on a tabulation of published information on selected responses to elevated CO_2 for ten leading crop species (Cure, 1985). The original tabulation includes interactions between CO_2 concentration and other important environmental factors and covers about 90 research reports. This is a summary of that tabulation in the form of predicted responses to a doubling of the current ambient CO_2 concentration from 340 to 680 p.p.m. It differs from Kimball's (1983) survey of plant yield response to a doubling of CO_2 concentration in that it examines the responses of fundamental processes underlying the yield response, as well as interactions between CO_2 and other factors.

METHODS

The species selected for the survey are listed in Table I. They represent broad classes of plants as well as being economically important crops and therefore relatively well studied. C_3 and C_4 grasses, root crops and annual broadleaf species, including legumes, probably represent categories or groups of species with fundamentally different responses.

The response variables which were surveyed are listed in Table II. They were chosen on the basis of their utility for modelling growth and yield response to high CO_2, rather than merely listing all the responses in the existing literature. This approach left blank spaces in the tables wherever information was lacking, thus highlighting our ignorance. Indeed, some response variables such as respiration were excluded from the tables because of the paucity of data for any species even though they are important in the adaptation of agriculture to the changing environment. In this paper we present only the tables showing the average response over all the experiments examined. Since the experiments varied greatly in the CO_2 concentrations and the units of measurement used, the results have been summarized as a predicted response to a doubled CO_2 concentration expressed as a percentage. Expressing the responses as percentages permits comparison of unlike variables (e.g., yield and conductance) within a species as well as across species. The number of studies and observations involved in each prediction are included and this provides a comprehensive picture of the data availability within each species/variable class as well as the relative responses.

TABLE I

Botanical character and agronomic significance of crop species selected for the Crop CO_2-Doubling Response Survey

Crop species	Botanical character				Use					Rank by acreage (USA)[a]	Rank by acreage (World)[a]
	Metabolism	Grass	Broad leaf	Legume	Grain	Forage/ Pasture	Root/ Tuber	Oil	Fiber		
Wheat *Triticum aestivum* L.	C_3	X			X					2	1
Barley *Hordeum vulgare* L.	C_3	X			X					6	4
Rice *Oryza sativa* L.	C_3	X			X					10	2
Corn *Zea mays* L.	C_4	X			X			X		1	3
Sorghum *Sorghum bicolor* (L.) Moench.	C_4	X			X	X				5	6
Soybean *Glycine max* (L.) Merr.	C_3		X	X	X			X		3	7
Alfalfa *Medicago sativa* L.	C_3		X	X		X				—	—
Cotton *Gossypium hirsutum* L.	C_3		X					X	X	7	9
Potato *Solanum tuberosum* L.	C_3		X				X			11	12
Sweet potato *Ipomoea batatas*	C_3		X				X			16	16

[a] The 1984 acreages for non-forage crops were ranked according to statistics from the Food and Agricultural Organization, United Nations Monthly Report 1984.

TABLE II

Response variables selected for the Crop CO_2-Doubling Response Survey

Short-term CER —	measurements of net carbon exchange rate made on leaves of plants grown at the ambient or control level of CO_2 and measured at elevated CO_2 concentrations.
Acclimitized CER —	measurements of net carbon exchange rate made on leaves of plants which have been growing at the elevated CO_2 concentration for at least a week.
Initial NAR —	net assimilation rate of plants calculated for an interval immediately following exposure to an elevated CO_2 concentration and not longer than (approximately) 2 weeks.
Long-term NAR —	net assimilation rate of plants calculated for an interval beginning $\geqslant$ 2 weeks after initial exposure to the elevated CO_2 concentration.
Biomass accumulation	
Root : shoot ratio	
Harvest index —	seed dry weight divided by total standing top dry weight unless noted otherwise (roots excluded).
Conductance	
Transpiration	
Yield	

Regressions

The relative responses from all the experiments within a species/variable class were regressed against CO_2 concentration using the General Linear Models procedure in SAS (Statistical Analytical Systems, Cary, NC). The intercepts of the curves are not presented because the models, which were always linear except where noted otherwise, were constrained to pass through a relative response of unity corresponding to the control value of CO_2. This was accomplished by subtracting 1 from all the relative responses, subtracting 340 from all the elevated CO_2 values and using the NOINT option in GLM. The predicted responses were then expressed as a percentage change. Exceptions to these procedures occurred for root:shoot ratio and harvest index, for which the regressions were based on simple differences between the values at elevated and control levels of CO_2.

Since the control values of unity were artificially generated when the relative responses were calculated, effective degrees of freedom for error were taken to be the degrees of freedom in the GLM output less the number of points at control CO_2 and the error mean square and confidence limits were calculated accordingly. For experiments in which the CO_2 control was outside the 300—350 p.p.m. range, a separate regression was run, a predicted relative response for 340 p.p.m. CO_2 was obtained and this value was used as the control. In a few cases a quadratic model fitted the data significantly better and, therefore, was adopted. These cases are indicated on the tables.

Pooling of data for overall responses

The overall response is the mean response to CO_2 doubling across any secondary treatments (interactions) which may have been present in the experiments. If there were no secondary treatments in a given experiment, the relative response values in each experiment were pooled with those from all other experiments within the species/variable class. If, however, there were other secondary treatments, e.g., light, temperature, water stress, or nutrient stress, values across these other treatments were averaged together to give a single, intermediate value for a given CO_2 level in that experiment. Variation from experiment to experiment was often larger than variation due to secondary treatments within an experiment and averaging across the secondary treatments ensured that the overall response for the class would not be biased towards those experiments in which there were many secondary treatments.

Pooling of data for interaction responses

Interaction responses are relative responses to CO_2 enrichment within various levels of the secondary treatments: water, nutrient, light and temperature, calculated separately. Even in experiments where many levels of a secondary treatment were used, one level was selected as the "control" value (for water stress or nutrient stress experiments) or "low" value (for light or temperature experiments) and another was selected to produce a contrasting "stress" or "high" value. These were then pooled with values obtained from other experiments in the species/variable class even though the treatments were often quite different. For instance, single episode water stress data were pooled with chronic water stress data. This crude handling of the data was necessary to construct a broadly based summary of research results on interactions of CO_2 and other important environmental variables.

RESULTS AND DISCUSSION

Overall responses

Although the empty cells in Tables III—VII are a crude measure of data availability, there is not a strict correspondence between a cell with an entry and a response which has been completely characterized. One begins to have confidence in a prediction only when several independent studies show a similar direction and order of magnitude of response. For example, we cannot place much confidence in the idea that doubling CO_2 concentration reduces potato biomass accumulation by 15% because it is based on only one study and the result is contrary to what has been found for most other species studied.

From Tables III—VII, the best studied species is clearly soybean (C_3

TABLE III

Crop CO_2-doubling response: overall

Response category	Wheat	Barley	Rice	Corn	Sorghum	Soybean	Alfalfa	Cotton	Potato	Sweet potato	Weighted average[b]
Short-term CER	+ 41 ± 7 (13,6)	+ 50 ± 31 (3,1)	+ 42 ± 19 (8,3)	+ 26 ± 9 (22,9)	− 3 ± [a] (2,1)	+ 78 ± 20 (19,8)	+ 139 ± [a] (2,1)	+ 60 ± 14 (13,4)	+ 105 ± 49 (3,1)	—	+ 52
Acclimatized CER	+ 27 ± 20 (10,5)	+ 14 ± [a] (2,1)	+ 46 ± [a] (2,1)	+ 4 ± 13 (9,3)	+ 6 ± 16 (5,2)	+ 42 ± 10 (39,16)	—	+ 13 ± 19 (9,4)	—	—	+ 29
Initial NAR	+ 11 ± 39 (3,1)	+ 14 ± [a] (2,1)	+ 26 ± 11 (8,3)	+ 9 ± 4 (10,5)	—	+ 35 ± 6 (15,7)	—	—	—	—	+ 23
Long-term NAR	+ 6 ± 31 (5,2)	+ 11 ± 7 (10,4)	—	+ 3 ± 9 (7,3)	+ 20 ± [a] (2,1)	+ 23 ± 5 (18,9)	—	+ 40 ± [a] (2,1)	+ 54 ± [a] (2,1)	+ 11 ± 25 (3,1)	+ 18
Biomass accumulation	+ 31 ± 16 (23,10)	+ 30 ± 17 (12,6)	+ 27 ± 7 (22,11)	+ 9 ± 5 (31,13)	+ 9 ± 29 (6,3)	+ 39 ± 5 (45,20)	+ 57 ± 277 (4,2)	+ 84 ± 126 (6,3)	− 15 ± [a] (2,1)	+ 59 ± 18 (3,1)	+ 30
Root:shoot ratio	+ 1.4 ± 3.2[c,d] (8,4)	+ 6.4 ± 6.9 (4,2)	− 4.0 ± [a] (2,1)	+ 3.1 ± 4.0[d] (11,5)	− 8.5 ± [a] (2,1)	+ 1.1 ± 1.0[d] (25,11)	− 5.0 ± 0.6 (4,2)	+ 3.2 ± 8.0 (5,2)	− 2.1 ± [a] (2,1)	+ 34.9 ± 14.6 (3,1)	+ 2.09
Harvest index	+ 2.4 ± 2.3[c,d] (12,6)	+ 1.3 ± [a] (2,1)	+ 1.9 ± 0.6 (6,3)	+ 4.3 ± 4.6[d] (5,2)	—	− 5.0 ± 4.4 (19,8)	—	—	+ 1.9 ± [a] (2,1)	—	− 0.39
Conductance	− 22 ± 29 (4,2)	− 52 ± 61 (3,1)	− 33 ± 7 (5,3)	− 37 ± 7 (13,5)	− 27 ± 45 (3,1)	− 31 ± 5 (21,7)	—	− 15 ± 32 (3,1)	− 59 ± 12 (3,1)	—	− 33
Transpiration	− 17 ± 17 (4,2)	− 19 ± 6 (7,3)	− 16 ± 9 (7,3)	− 26 ± 6 (15,6)	− 27 ± 16 (6,2)	− 23 ± 5 (19,8)	—	− 18 ± 17 (7,3)	− 51 ± 24 (3,1)	—	− 23
Yield	+ 35 ± 14[d] (17,8)	+ 70 ± [a] (2,1)	+ 15 ± 3 (6,3)	+ 29 ± 64 (3,1)	—	+ 29 ± 8 (28,12)	—	+ 209 ± [a] (2,1)	+ 51 ± 111 (6,3)	+ 83 ± 12 (3,1)	+ 41

Data represent the percentage change at 680 p.p.m. CO_2 compared with controls (300—350 p.p.m.) ± 95% confidence limits, as estimated by regression analysis. Exceptions are harvest index and root:shoot ratio, for which absolute changes are predicted. The values in parentheses are the number of relative response values used in each regression and the number of studies supplying those values.

[a]In cases where results were based on only two data points, error degrees of freedom were 0 and confidence limits could not be calculated. [b]For the weighted average for a response category, each predicted response value was multiplied by the number of studies associated with it, then these were summed and divided by the total number of studies in the response category row. [c]All values for root:shoot ratio and harvest index and their confidence limits should be multiplied by 10^{-2}. [d]Based on quadratic model.

TABLE IV

Crop CO_2-doubling response: water stress interactions

Response category	Wheat	Barley	Rice	Corn	Sorghum	Soybean	Alfalfa	Cotton	Potato	Sweet potato
Short-term CER	—	—	—	—	—	—	—	—	—	—
Acclimatized CER	—	—	—	—	—	C: + 65 ± 29 S: + 38 ± 16 (5,2)	—	—	—	—
Initial NAR	—	—	—	—	—	—	—	—	—	—
Long-term NAR	—	—	—	—	—	—	—	—	—	—
Biomass accumulation	C: + 35 ± 34 S: + 33 ± 30 (8,4)	C: + 107 ± [a] S: + 65 ± [a] (2,1)	C: + 51 ± [a] S: + 52 ± [a] (2,1)	C: + 0 ± [a] S: + 36 ± [a] (2,1)	C: + 26 ± [a] S: + 31 ± [a] (2,1)		C: + 130 ± [a] S: + 78 ± [a] (2,1)	C: + 0 ± [a] S: + 19 ± [a] (2,1)	—	—
Root:shoot ratio	C: − 4.1 ± [a,b] S: − 3.2 ± [a] (2,1)	C: + 1.0 ± [a] S: − 4.0 ± [a] (2,1)	C: − 3.0 ± [a] S: − 5.0 ± [a] (2,1)	C: − 26.0 ± [a] S: − 5.0 ± [a] (2,1)	C: − 8.0 ± [a] S: − 9.0 ± [a] (2,1)	—	C: + 2.0 ± [a] S: − 12.0 ± [a] (2,1)	C: + 10.0 ± [a] S: + 2.0 ± [a] (2,1)	— —	— —
Harvest index	C: + 2.8 ± 3.1[b] S: + 2.8 ± 11.8 (4,2)	—	—	—	—	C: + 1.6 ± [a] S: + 2.7 ± [a] (2,1)	—	—	—	—
Conductance	—	—	—	—	—	C: − 23 ± 3 S: − 32 ± 68 (3,1)	—	—	—	—
Transpiration	—	—	—	—	—	C: − 14 ± [a] S: − 12 ± [a] (2,1)	—	—	—	—
Yield	C: + 25 ± 151 S: + 41 ± 250 (4,2)	—	—	—	—	C: + 60 ± [a] S: + 46 ± [a] (2,1)	—	—	—	—

Data represent the percentage change at 680 p.p.m. CO_2 compared with controls (300—350 p.p.m.) ± 95% confidence limits, as estimated by regression analysis. Exceptions are harvest index and root : shoot ratio, for which absolute changes are predicted. The values in parentheses are the number of relative response values used in each regression and the number of studies supplying those values. C = control: S = stress.

[a] In cases where results were based on only two data points, error degrees of freedom were 0 and confidence limits could not be calculated.

[b] All values for root : shoot ratio and harvest index and their confidence limits should be multiplied by 10^{-2}.

broadleaf), followed by wheat (C_3 grass) and corn (C_4 grass). The root crops are the least well studied, probably because of their lesser economic importance at present (Table I). However, there is some evidence that root crops may be among those which respond most strongly to CO_2 enrichment (Kimball, 1983) and their relative importance as crops may therefore increase as CO_2 concentration increases.

Carbon assimilation

The data for CER (CO_2 exchange rate) and NAR (net assimilation rate), were divided into short-term and long-term categories, reflecting the importance of time for these measurements.

In the overall crop response to doubled CO_2 concentration (Table III) the weighted average short-term CER response is about + 52%, whereas acclimatized CER is of the order of + 29%. Soybean and cotton are the only species for which photosynthesis has been studied explicitly as a function of time of exposure or acclimatization to elevated CO_2 and these studies (Mauney et al., 1979; Wong, 1980; Clough and Peet, 1981; Peet, 1984; DeLucia et al., 1985) support the more general observation made here. Although CER always fell with time for soybeans, in most studies it remained higher in high than in low CO_2, although in a few studies it fell to about the same level or even lower. Data for cotton support this picture. The data for wheat, barley, rice and corn are also in general agreement, but since (unlike soybean and cotton) short-term CER data and acclimatized CER data were collected by different investigators under different conditions, these do not provide direct confirmation. The CER response categories include leaf as well as canopy measurements and thus could be misleading. Gifford (1977) showed in a growth chamber study that photosynthetic increases for wheat plants grown in a 490 p.p.m. CO_2 atmosphere were 56% for the flag leaf, 40% for the plant canopy and 238% on a unit ground area basis, respectively, compared with controls grown at 290 p.p.m. CO_2. Although the last value is in the form most appropriate for crop predictions, this kind of data has been difficult to obtain and is therefore rare.

NAR is in some ways a more useful measure of net carbon input as it averages over days or weeks and is a simpler measurment to make and therefore less subject to error. Since the effects of dark respiration are by definition included in NAR, initial NAR responses were smaller than CER responses for all the species studied. The apparent reversal of this trend for sorghum cannot be trusted because it is based on such few studies.

For soybean, NAR also fell with time at any CO_2 level, with NAR of high CO_2 plants falling as fast or faster than that of controls (Patterson and Flint, 1982; Sionit et al., 1982, Sionit, 1983; Rogers et al., 1984a). The few studies directly addressing the issue have shown that high metabolic or storage "sink" (carbon utilization) activity is required for the photosynthetic response to elevated CO_2 to be sustained (Clough and Peet, 1981; Peet, 1984). In a classic growth study, Neales and Nicholls (1978) clearly described

TABLE V

Crop CO_2-doubling response: nutrient stress interactions

Response category	Wheat	Barley	Rice	Corn	Sorghum	Soybean	Alfalfa	Cotton	Potato	Sweet potato
Short-term CER	—	—	—	—	—	—	—	C: + 76 ± [a] S: + 59 ± [a] (2,1)	—	—
Acclimatized CER	—	—	—	C: + 32 ± 46 S: + 29 ± 43 (3,1)	—	C: + 39 ± [a] S: + 14 ± [a] (2,1)	—	C: + 35 ± 109 S: + 23 ± 35 (4,2)	—	—
Initial NAR	—	—	—	C: + 5 ± [a] S: + 3 ± [a] (2,1)	—	C: + 35 ± 73 S: + 45 ± 11 (4,2)	—	—	—	—
Long-term NAR	C: + 25 ± [a] S: + 31 ± [a] (2,1)	—	—	—	—	C: + 19 ± 123 S: + 35 ± 102 (4,2)	—	—	—	—
Biomass accumulation	C: + 39 ± 15 S: + 10 ± 2 (4,2)	—	C: + 32 ± 69 S: + 30 ± 21 (4,2)	C: + 14 ± 7 S: + 11 ± 6 (6,3)	—	C: + 52 ± 73 S: + 40 ± 60 (6,3)	C: + 13 ± [a] S: + 18 ± [a] (2,1)	C: + 146 ± [a] S: + 133 ± [a] (2,1)	—	—
Root:shoot ratio	C: + 1.0 ± 0.5[b] S: + 2.5 ± 4.4 (4,2)	—	—	C: − 1.9 ± [a] S: + 5.2 ± [a] (2,1)	—	C: − 0.3 ± 3.2 S: − 3.2 ± 12.5 (6,3)	C: − 9.6 ± [a] S: − 2.7 ± [a] (2,1)	—	—	—
Harvest index	C: + 2.7 ± 14.7[b] S: + 1.6 ± 15.1 (4,2)	—	—	—	—	C: − 5.1 ± [a] S: − 0.0 ± [a] (2,1)	—	—	—	—
Conductance	—	—	—	—	—	C: − 37 ± [a] S: − 45 ± [a] (2,1)	— —	— —	— —	— —

Transpiration	—	—	—	C: − 47 ± [a] S: − 49 ± [a] (2,1)	—	C: − 28 ± [a] S: − 36 ± [a] (2,1)	—	C: − 33 ± 30 S: − 41 ± 24 (4,2)	—	—
Yield	C: + 43 ± 57 S: + 16 ± 18 (4,2)	—	—	—	—	C: + 126 ± [a] S: + 102 ± [a] (2,1)	—	—	—	—

Data represent the percentage change at 680 p.p.m. CO_2 compared with controls (300—350 p.p.m.) ± 95% confidence limits, as estimated by regression analysis. Exceptions are harvest index and root:shoot ratio, for which absolute changes are predicted. The values in parentheses are the number of relative response values used in each regression and the number of studies supplying those values. C = control; S = stress.

[a] In cases where results were based on only two data points, error degrees of freedom were 0 and confidence limits could not be calculated.

[b] All values for root:shoot ratio, harvest index and their confidence limits should be multiplied by 10^{-2}.

TABLE VI

Crop CO_2-doubling response: light interactions

Response category	Wheat	Barley	Rice	Corn	Sorghum	Soybean	Alfalfa	Cotton	Potato	Sweet potato
Short-term CER	L: + 37 ± 20 H: + 49 ± 26 (3,1)	—	—	L: + 21 ± 11 H: + 23 ± 16 (7,3)	—	L: + 52 ± 51 H: + 100 ± 32 (7,3)	—	L: + 67 ± 14 H: + 47 ± 28 (6,2)	—	—
Acclimatized CER	—	L: + 11 ± [a] H: + 15 ± [a] (2,1)	—	—	—	L: + 84 ± 23 H: + 62 ± 25 (12,6)	—	—	—	—
Initial NAR	—	L: + 9 ± [a] H: + 18 ± [a] (2,1)	L: + 39 ± [a] H: + 26 ± [a] (2,1)	L: + 8 ± [a] H: + 12 ± [a] (2,1)	—	L: + 23 ± [a] H: + 31 ± [a] (2,1)	—	—	—	—
Long-term NAR	—	L: + 7 ± 26 H: + 7 ± 7 (6,3)	—	L: − 3 ± [a] H: + 9 ± [a] (2,1)	—	—	—	—	—	—
Biomass accumulation	L: + 15 ± [a] H: + 20 ± [a] (2,1)	L: + 20 ± 32 H: + 17 ± 14 (4,2)	L: + 28 ± [a] H: + 31 ± [a] (2,1)	L: + 16 ± 32 H: + 19 ± 22 (4,2)	—	L: + 44 ± 175 H: + 41 ± 73 (4,2)	—	—	—	—
Root:shoot ratio	—	—	—	L: + 2.0 ± [ab] H: + 1.5 ± [a] (2,1)	—	L: − 2.0 ± [a] H: − 1.0 ± [a] (2,1)	—	—	—	—
Harvest index	—	—	—	—	—	—	—	—	—	—
Conductance	L: − 31 ± [a] H: − 25 ± [a] (2,1)	—	—	L: − 34 ± 23 H: − 40 ± 17 (5,2)	—	—	—	—	—	—

Transpiration	L: − 27 ± [a] H: − 11 ± [a] (2,1)	—	—	L: − 30 ± 19 H: − 28 ± 15 (5,2)	—	L: − 7 ± 78 H: − 15 ± 7 (4,2)	—	—	—	—
Yield	—	—	—	—	—	—	—	—	—	—

Data represent the percentage change at 680 p.p.m. CO_2 compared with controls (300–350 p.p.m) ± 95% confidence limits, as estimated by regression analysis. Exceptions are harvest index and root:shoot ratio, for which absolute changes are predicted. The values in parentheses are the number of relative response values used in each regression and the number of studies supplying those values. L = Low: H = High.

[a] In cases where results were based on only two data points, error degrees of freedom were 0 and confidence limits could not be calculated.

[b] All values for root:shoot ratio, harvest index and their confidence limits should be multiplied by 10^{-2}.

TABLE VII

Crop CO_2-doubling response: temperature interactions

Response category	Wheat	Barley	Rice	Corn	Sorghum	Soybean	Alfalfa	Cotton	Potato	Sweet potato
Short-term CER	L: + 6 ± 4 H: + 52 ± 35 (4,2)	—	—	—	—	—	L: +96 ± [a] H: + 177 ± [a] (2,1)	L: + 100 ± 28 H: + 90 ± 27 (3,1)	—	—
Acclimatized CER	—	—	—	—	—	L: + 72 ± 95 H: + 80 ± 20 (4,2)	—	—	—	—
Initial NAR	—	—	L: + 24 ± [a] H: + 34 ± [a] (2,1)	L: + 8 ± [a] H: + 12 ± [a] (2,1)	—	L: + 24 ± [a] H: + 31 ± [a] (2,1)	—	—	—	—
Long-term NAR	—	—	—	—	—	—	—	—	—	—
Biomass accumulation	—	—	L: + 26 ± [a] H: + 36 ± [a] (2,1)	L: + 12 ± [a] H: + 18 ± [a] (2,1)	—	L: + 27 ± [a] H: + 39 ± [a] (2,1)	—	—	—	—
Root:shoot ratio	—	—	—	—	—	—	—	—	—	—
Harvest index	—	—	—	—	—	—	—	—	—	—
Conductance	—	—	—	—	—	—	—	—	—	—
Transpiration	—	—	—	—	—	L: − 9 ± [a] H: − 13 ± [a] (2,1)	—	—	—	—
Yield	—	—	—	—	—	—	—	—	—	—

Data represent the percentages change at 680 p.p.m. CO_2 compared with controls (300–350 p.p.m.) ± 95% confidence limits, as estimated by regression analysis. Exceptions are harvest index and root:shoot ratio, for which absolute changes are predicted. The values in parentheses are the number of relative response values used in each regression and the number of studies supplying those values. L = low; H = high.

[a] In cases where results were based on only two data points, error degrees of freedom were 0 and confidence limits could not be calculated.

a similar response for wheat and other data for wheat and barley are also consistent (Ford and Thorne, 1967; Sionit et al., 1981).

All of the data for the carbon assimilation variables for C_3 species (Table III) taken together suggest that the grasses may respond somewhat less strongly to elevated CO_2 concentrations than the broadleaf species soybean and cotton. However, even in this first, relatively well studied category of carbon assimilation, we are unable to make a concrete statement about the broader categories of grass versus broadleaf species because of sparse data and large variability.

Corn showed a surprisingly high initial CER response considering that it already possesses a CO_2-concentrating mechanism (the C_4 metabolic pathway) in its leaves. Carbon assimilation responses to a doubling of CO_2 concentration ranged from -5% to around $+40\%$ and it is not clear what environmental factors may have caused this variability. All the carbon assimilation variables for corn and sorghum taken together, however, confirm that the C_4 crops respond very much less than the C_3 crops in this category.

Biomass accumulation

For most of the species surveyed, the average predicted increase in biomass accumulation for a doubling of CO_2 concentration was greater than the increase in long-term NAR. This is probably attributable to the increased leaf area of plants growing in high concentrations of CO_2, which compounds the effect of NAR in producing higher biomass.

The effects of CO_2 doubling on biomass accumulation among C_3 grasses appear to be reasonably similar at about $+28\%$, but the data for C_3 broadleaf species are sparse and erratic. If soybean may be taken to represent C_3 broadleaf crops, the effect on biomass accumulation of doubling CO_2 concentration appears to be higher than for the C_3 grasses, which is in keeping with their carbon assimilation responses. Biomass response to CO_2 doubling was low for the C_4 species corn ($+9\%$) and sorghum ($+3\%$) which also agrees with the generally low response of carbon assimilation for these species.

Harvest index and yield

For soybean and wheat, the only species for which a number of studies exist, yield results were similar to the biomass accumulation results. The relationships between biomass accumulation and yield for these two species are consistent with their predicted changes in harvest index (*HI*), $+0.02$ units for wheat and -0.05 units for soybean. Soybean is the only species for which *HI* consistently decreased as CO_2 concentration increased, an observation which raises questions about the efficiency of carbohydrate partitioning in soybean leaves during reproductive growth. The decreases in *HI* for soybean skewed the weighted average for *HI* for all species.

Yield data for the C_3 grasses are few and variable. The value for rice is to be regarded with caution since none of the three studies included a proper control treatment.

Conductance and transpiration

The responses of conductance and transpiration to a doubling of CO_2 concentration were surprisingly uniform across species. The decrease in transpiration is not as large as the decrease in conductance because, as the stomata close and transpiration begins to fall, leaf temperature tends to increase, which in turn increases transpiration again. It is important to note that these changes are for leaf conductance and transpiration rates. Crop water use may not change in the same way because the increase in canopy leaf area may compensate for lower leaf transpiration rate in the high CO_2 (Jones et al., 1985; Rogers et al., 1984b).

Interactions

Judging by the availability of data in the cells of Tables IV—VII, water stress, which is probably the most important of the environmental interactions with elevated CO_2, is one of the least well studied. Because elevated CO_2 tends to lower leaf conductance (Table III), water use is reduced and water stress may be avoided if a drought period is of short duration. This effect may be partly offset by an increase in leaf area as well as a rise in leaf temperature, which increases the vapor pressure gradient for transpiration. Under conditions of prolonged stress, however, stomatal conductance will eventually fall to near zero in any CO_2 concentration. It is important to obtain realistic estimates from field-grown plants of leaf area response to elevated CO_2 as a step towards anticipating changes in crop water use under field conditions. Differences among the experiments in leaf area response to CO_2 probably account for the different relative yield responses to CO_2 with and without water stress (Table IV).

Several investigations have shown that uptake of some nutrients does not keep pace with the increased growth which occurs with increased CO_2 concentration. However, among the few papers reporting CO_2 responses at varying nutrient concentrations, very few investigate possible mechanisms of interaction on nutrient uptake, growth, or physiological processes, or even report tissue nutrient concentrations. In the categories of carbon assimilation, biomass accumulation and yield (Table V), a majority of entries show that nutrient stress — often resulting from dilutions of complete nutrient solutions rather than of selected nutrients — limits the effects of CO_2 enrichment. Growth requirements for major nutrients during CO_2-enhanced growth are almost entirely lacking for any species.

The absolute increase in photosynthetic rate in response to CO_2 concentration is always greater in high light than in low light. However, this is not necessarily true of the relative increase. Crop studies in which the influence of light on the CO_2 response of CER, NAR and growth are reported showed no consistent pattern, either within or among species (Table VI). High light increased the relative response to CO_2 in about one-third of the studies, decreased it in another third and had no effect in the remainder. In two studies, high light had a positive effect on the relative response of NAR to CO_2 concentration when the plants were young, with this effect becoming zero or negative as the plants aged (barley, Ford and Thorne, 1967; corn, Sionit et al., 1982).

In all except one study, responses to CO_2 were larger at high temperature than at low (Table VII). In most cases, the effect of temperature on the CO_2 response of CER, NAR and biomass accumulation was measured at high light intensity. Under these conditions, the relative increases due to elevated CO_2 concentration were greater at high temperatures up to and in most cases beyond the optimum temperature (that temperature in each study at which the measured variable had the highest value). At low light intensity, however, the effect of high temperature on the CO_2 response was less positive.

CONCLUSIONS AND RECOMMENDATIONS

(1) The statistical approach taken in this study requires a large number of independent data entries to arrive at a reliable estimate of a CO_2 doubling response. Table III shows that we may begin to consolidate our understanding of the overall direction of change of key physiological processes of different crop species growing under constant conditions of elevated CO_2. However, the conclusions drawn with respect to overall responses are more reliable than those for interactions. Indeed, these tables highlight the paucity and variability of data on interactions between CO_2 and other environmental variables. This review reveals that there is just too little quantitative information available to enable us to predict precise response to CO_2 concentration under well-defined environmental conditions.

(2) Although the carbon assimilation variables for C_3 broadleaf species show stronger responses to elevated CO_2 than the C_3 grasses, the data are as yet too erratic and sparse to firmly delineate or characterize response groups based on growth form.

(3) The C_4 plants, corn and sorghum, showed a smaller increase in carbon assimilation and growth than C_3 plants. In view of the presence of the CO_2-concentrating mechanism in C_4 leaves, this smaller response to an increase in CO_2 concentration is not surprising. Indeed it is surprising that there was any response to high CO_2. We need to examine possible roles of increased turgor or leaf temperature in determining the final extent of C_4 canopy development.

(4) Soybeans and wheat are relatively well represented in the tables. Further information on the growth response of the other species is required. Several independent studies are necessary to obtain reliable information about a crop because of the variability in experimental conditions.

(5) Root:shoot ratios generally increased only a small amount.

(6) For all species except soybeans, *HI* increased under elevated CO_2 concentrations, thus compounding the increases in biomass accumulation in

determining increased yield. Future breeding efforts will probably correct the situation for soybean *HI*, thus further increasing soybean yield.

(7) Conductance was decreased by CO_2 doubling rather uniformly across species by about 34%. Future crop water consumption, however, is difficult to predict due to uncertainty about leaf area response to high CO_2 under natural field conditions. To remove this impediment, realistic estimates of leaf area responses to elevated CO_2 under field conditions are necessary.

(8) Many of the plants in controlled environment studies showed greater responses to CO_2 than plants grown in other systems. Whereas a fundamental understanding of CO_2 interactions with water availability, nutrition level, light and temperature can most readily be obtained in controlled environments, only field trials of the major crops can validate model predictions with respect to all of the processes discussed above.

REFERENCES

Clough, J.M. and Peet, M.M., 1981. Effects of intermittent exposure to high atmospheric CO_2 on vegetative growth in soybean. Physiol. Plant., 53: 565—569.

Cure, J.D., 1985. Carbon dioxide doubling responses: a crop survey. In: Strain, B.R. and Cure, J.D. (Editors), Direct Effects of Increasing Carbon Dioxide on Vegetation (DOE/ER-0238). Chap. 5 and Appendix. U.S. Dep. Energy, Washington, D.C. Available from NTIS, Springfield, VA 22161.

Dahlman, R.C., Strain, B.R. and Rogers, H.H., 1985. Research on the response of vegetation to elevated atmospheric carbon dioxide. J. Environ. Qual., 14: 1—8.

DeLucia, E.H., Sasek, T.W. and Strain, B.R., 1985. Photosynthetic inhibition after long-term exposure to elevated levels of atmospheric carbon dioxide. Photosynth. Res., 7: 175—184.

Ford, M.A. and Thorne, G.N., 1967. Effect of CO_2 concentration on growth of sugar-beet, barley, kale, and maize. Ann. Bot., 31: 629—644.

Gifford, R.M., 1977. Growth pattern, carbon dioxide exchange and dry weight distribution in wheat growing under differing photosynthetic environments. Aust. J. Plant Physiol. 4: 99—110.

Jones, P., Allen, L.H., Jr., Jones, J.W. and Valle, R., 1985. Photosynthesis and transpiration responses of soybean canopies to short- and long-term CO_2 treatments. Agron. J., 77: 119—126.

Keeling, C.D., 1983. The global carbon cycle: What we know and could know from atmospheric, biospheric and oceanic observation. Proc. CO_2 Res. Conf., Berkely Springer, WV, (DOE-CONF 820970), available from NTIS, Springfield, VA 22161.

Kimball, B.A., 1983. Carbon dioxide and agricultural yield: an assemblage and analysis of 430 prior observations. Agron. J., 75: 779—788.

Mauney, J.R., Guinn, G., Fry, K.E. and Hesketh, J.D., 1979. Correlation of photosynthetic carbon dioxide uptake and carbohydrate accumulation in cotton, soybean, sunflower and sorghum. Photosynthetica, 13: 260—266.

Neales, T.F. and Nicholls, A.O., 1978. Growth responses of young wheat plants to a range of ambient CO_2 levels. Aust. J. Plant Physiol., 5: 45—59.

Patterson, D.T. and Flint, E.P., 1982. Interacting effects of CO_2 and nutrient concentration. Weed Sci., 30: 389—394.

Peet, M.M., 1984. CO_2 enrichment of soybeans. Effect of leaf/pod ratio. Physiol. Plant., 60: 38—42.

Rogers, H.H., Cure, J.D., Thomas, J.F. and Smith, J.M., 1984a. Influence of elevated CO_2 on growth of soybean plants. Crop Sci., 24: 361—366.
Rogers, H.H., Sionit, N., Cure, J.D., Smith, J.M. and Bingham, G.E., 1984b. Influence of elevated carbon dioxide on water relations of soybeans. Plant Physiol., 74: 233—238.
Sionit, N., 1983. Response of soybean to two levels of mineral nutrition in CO_2-enriched atmosphere. Crop Sci., 23: 329—333.
Sionit, N., Mortensen, D.A., Strain, B.R. and Hellmers, H., 1981. Growth response of wheat to CO_2 enrichment and different levels of mineral nutrition. Agron. J., 73: 1023—1027.
Sionit, N., Hellmers, H. and Strain, B.R., 1982. Interaction of atmospheric CO_2 enrichment and irradiance on plant growth. Agron. J., 74: 721—725.
U.S. National Research Council, 1983. Changing Climate. National Academy Press, Washington, D.C., 496 pp.
Wong, S.C., 1980. Effects of elevated partial pressure of CO_2 on rate of CO_2 assimilation and water use efficiency in plants. In: Pearman, G.I., (Editor), Carbon Dioxide and Climate, Australian Research. Aust. Acad. Sci., Canberra, Australia, pp. 159—166.